AMAZONIANA	I	4	287—302	Kiel, Dez. 1968

(From: Max-Planck-Institut für Limnologie, Abt. Tropenökologie, Plön/H., Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil)

Litter Production in an Area of Amazonian Terra Firme Forest. Part I. Litter - fall, Organic carbon and total Nitrogen Contents of Litter[1]).

by Hans Klinge

Pedologist, MPI of Limnology, Department of Tropical Ecology, Plön

and

William A. Rodrigues

Head, Forest Research Division, I.N.P.A., Manaus.

Contents

Abstract

In 1963 and 1964 litter was collected in a terra firme forest near Manaus, oven-dried and shipped to Europe. The samples were subdivided into four litter fractions (leaves, wood, fruits, termite fraction), dried at 105° and weighed. Organic carbon and total nitrogen of these litter fractions were determined.

Annual average litter production is 7.4 t/ha consisting in 5.6 t of leaves, and 1.8 t of other litter. 105.6 kg nitrogen return annually to the soil. Compared with data on litter production and nitrogen content of litter of other tropical forests, the Amazonian forest produces less litter and returns a lower amount of nitrogen to the soil.

Introduction

As recently shown by Bray and Gorham (1964) there are no data on litter production of equatorial lowland forest of Amazonia, there being scanty determinations in rain forests of other tropical regions (Laudelout 1961).

[1]) Partially supported by the Conselho Nacional de Pesquisas.

In 1962, co-operation in measuring and analyzing the litter of an Amazonian terra firme forest (evergreen tropical rain forest) of the Manaus area was arranged by both authors.

In this contribution, part I, data on the production of both total litter and litter fractions, and their carbon and nitrogen contents as well, are presented. In part II, the nutrient content (phosphorus, potassium, sodium, calcium and magnesium) of the litter is dealt with.

Litter collection technique

In 1963 and 1964, ten wooden litter collectors, each of 0.25 sq.m. in area, were placed directly on the ground within half a hectare of the Walter Egler Forest Reserve, northeast of Manaus. Litter was collected at weekly intervals, oven-dried and weighed. Samples of four succeeding weeks corresponding more or less to one month, were subsequently unified.

In 1963, litter collection suffered from theft of litter collectors. All remained litter samples of each collector were unified, prior to analysis. The results were subsequently calculated for a 52-weeks-year. — In 1964, only very exceptionally litter collectors disappeared from the forest.

In 1965, the collection of oven-dry samples of both years was shipped to Europe where it has been immediately analyzed, in the Soils Laboratory of the Max Planck Institute of Limnology.

Analytical procedures

Samples were thoroughly subdivided by hand, into three litter fractions:

i) Leaves (subsequently referred to as "leaves"),

ii) Branches, twigs, and bark (subsequently referred to as "wood"), and

iii) Fruits, flowers, bud scales, seeds, etc., and non-reckognizable plant rests as well (subsequently referred to as "fruits").

From few samples, hard, dark clayey crumbles were obtained which have been attributed to termite activity (fraction iv) "termite fraction").

The litter fractions were subsequently milled in a commercial coffee mill, dried at 105° C and weighed. Before milling, leaves were grounded in a commercial mixer, and hard material of the fractions ii), iii) and iv) was cracked with a hammer or broken by hand.

With respect to the smallness of fractions ii), iii) and iv), some four-week samples were mixed together, prior to analysis, in order to obtain a sufficient amount of material within each sample to be analyzed.

Humidity of milled samples was determined and controlled as well by aid of a CENCO Moisture Balance.

If not otherwise indicated, analytical data are given in metric weight units (kg, t), on an oven-dry basis.

Total organic carbon was determined by wet combustion with chromic acid, and colorimetrically estimated (Riehm and Ulrich 1950), using a Zeiss Spectrophotometer PMQ II. No correction factor was used to convert carbon values into organic matter. The Kjeldahl technique was used to estimate total nitrogen.

The site and its forest cover

The Walter Egler Forest Reserve is located to the northeast of the Manaus-Itacoatiara road, at km 65. Its forest is a typical Amazonian upland rain forest on loamy soil. Floristically and physiognomically, it may be considered the same type of forest community as that found at Manaus.

Recently, a forest inventory of 137,000 hectares was conducted by Rodrigues (1967) along the Manaus-Itacoatiara road, which included the Walter Egler forest. This data are very useful for general forest characterization of the site where the litter-fall was measured. This inventory counted only the trees 25 cm and over in diameter at breast height.

The forest is very dense, since it has an average of 102 trees per hectare. The mean height of its main canopy is about 25 m high. Structurally, the forest (Photo 1 and 2) may be separated, but not clearly so, into 5 strata. The upper 3 strata are rather discontinuous and ill-defined vertically. The 2 highest strata together form the main canopy of the forest. Emergent trees are uncommon. The lowest tree stratum consists mainly of young trees of the higher strata and of small species peculiar to this layer. The undergrowth is formed by the shrub and ground strata. Both these strata are continuous, but normally not so dense. Their stratification is not well defined vertically. The shrub stratum consists mainly of many saplings, some true shrubs, small palms, etc. The constituents of the ground stratum include mainly tree seedlings, many stemless palms, a few herbaceous plants, undershrubs, some *Trichomanes* and, occasionally, *Selaginella* occurs in lighter places.

Large woody lianes are always very common in the undisturbed forest, where they generally ascend to the canopy, and often link two or more trees. There are many species of lianes. In the undergrowth, some young lianes and small climbers are frequent, e. g. *Ampeliziziphus amazonicus*, *Abuta grandifolia*, *Strychnos* spp., *Ischnosiphon* spp., etc.

The forest, under normal conditions, contains relatively few vascular epiphytes. Inside the forest there are a few shade epiphytes, specially small ferns. Mosses, algae and lichens are relatively abundant on the stems of many species. Sun epiphytes, representing many genera and species, particularly Bromeliaceae, Araceae and Orchidaceae, are more frequent. They perch on the trunks, along the larger branches, and in the centre of the crowns of some of the taller trees. On the ground, the only saprophyte commonly found is one or more species of *Leiphaimos*.

The crowns of the tallest trees tend to be very wide and umbrella-shaped as in *Parkia pendula*, *Pithecolobium pedicellare*, *Anacardium parvifolium*, *Dinizia excelsa*, *Dipteryx odorata* etc. The crowns of these species are frequently up to 40 m wide. The crowns of the lowest trees are small and are usually deeper than wide. The majority is conical.

The largest trees generally have trunks not thicker than 150 cm in diameter. The diameter of the majority of trees ranges from 25 to 54 cm (92%). 54% of the trees have diameters between 25 and 34 cm (see figure 1).

Abb. 1: Profile of a typical Amazonian upland rain forest near the Walter Egler Forest Reserve, on the Manaus-Itacoatiara road, Km. 66 — Amazonas.

Abb. 2: The undergrowth of the Walter Egler Forest Reserve, Amazonas, a typical Amazonian rain forest, showing the large number of seedlings, saplings, stemless palms, small trees, shrubs and herbs.

Abb. 3: A wooden litter collector of 0,25 m² on the ground in the Walter Egler Forest Reserve, Amazonas. Note the dense layer of litter on the ground.

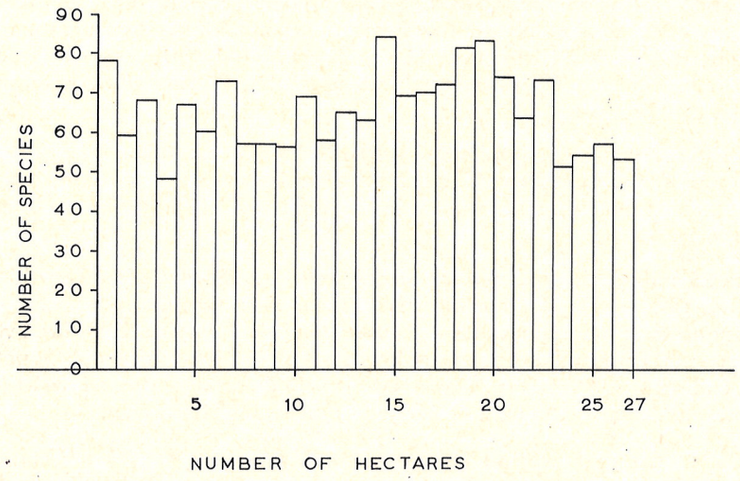

Fig. 1: Distribution of the tree species 25 cm and over in diameter per hectare from the rain forest along the Manaus-Itacoatiara road, Amazonas.

From an economic point of view the average volume of merchantilable wood of trees 25 cm and over in diameter is about 102 m³ per hectare. The mean volume per tree is about 1 m³. Trees of large volume are very few. The largest ones are not generally over 90 m³ of wood (*Dinizia exelsa*).

During the dry season, so-called "summer", from June to October, most trees change their foliage. This is most striking in the highest canopy where one can see most trees totally defoliated or nearly so for a few days or weeks. This occurs most commonly just before or during the flowering or the fruiting. Others get new leaves almost simultaneously with the fall of the old ones. The leaf-fall is facultative in most of these species. Yet, it is in the dry season or at the beginning or the end of this season, that most trees blossom. Most species bear fruit in the rainy season or "winter" (January to May). However, one finds some species flowering and/or fruiting in every month of the year.

The most important deciduous trees observed around Manaus are *Hymenaea intermedia*, *Cariniana micrantha*, *Piptadenia suaveolens*, *Astronium lecointei*, *Hymenolobium* spp., *Vatairea* spp., *Caryocar glabrum*, *Dipteryx odorata*, *Platymiscium duckei*, *Tabebuia* spp., *Parkia pendula*, *Parkia multijuga*, *Pithecolobium pedicellare*, *Copaifera multijuga*, *Peltogyne catingae* var. *glabra*, *Buchenavia* spp. and many others.

Plank buttresses and depply fluted trunks are an highly characteristic feature of some large trees of the upper strata. The trees with these features constitute about 5% of all trees of a diameter of 25 cm and above. Deeply fluted trunks occur in some species of *Aspidosperma*, *Swartzia* and *Sloanea*. Two species, *Geissospermum sericeum* and *Minquartia guianensis*, which are frequent in the upland forest, have characteristic deeply sulcate boles for their entire length. Large buttressed trees have been observed in *Dinizia excelsa*, *Buchenavia huberi*, *B. viridiflora*, *Peltogyne catingae* var. *glabra*, *Ragala spuria* and others. Stilt rooted trees are quite common in the swamp forests, e. g. *Symphonia globulifera*, *Socratea exorrhiza*, *Tovomita* spp. In the well-drained forest stilt roots are common in *Sloanea synandra* and in one species of *Tovomita*.

Floristically, the forest is very heterogeneous. About 470 species of trees with a diameter of 25 cm and above were counted in the forest inventory. This number does not give an accurate idea of the total number of tree species, since in addition there are many species which did not enter into the inventory. The average number of species per hectare was 65 (see Figures 2a and 2b). 50% of the total individual trees 25 cm and over counted were represented by 43 species.

The floristic composition, considering only the 10 most abundant species separately of each group of trees from 25 to 45 cm and over in diameter, is represented respectively by 24 and 25% of the total trees counted in the inventory. These species are listed below for each group.

a) Trees 25 and over in diameter: matamatá preto — *Eschweilera odora* (Lecythidaceae); ripeiro vermelho — *Corythophora alta* (Lecythidaceae); Cuquirana brava — *Ragala spuria* (Sapotaceae); macucu murici — *Vantanea parvifolia* (Humiriaceae); breu vermelho — *Protium* spp. (Burseraceae); rosada brava — *Micropholis guianensis* (Sapotaceae); abiurana fedorenta — *Pouteria* sp. (Sapotaceae); uchi de cotia — *Parinari excelsa* (Chrysobalanaceae); and acariquara roxa — *Minquartia guianensis* (Olacaceae).

b) Trees 45 cm and over in diameter: cupiúba — *Goupia glabra* (Celastraceae); cardeiro — *Scleronema micranthum* (Bombacaceae); ripeiro vermelho — *Corythophora alta* (Lecythidaceae); matamá preto — *Eschweilera odora* (Lecythidaceae); Louro preto —

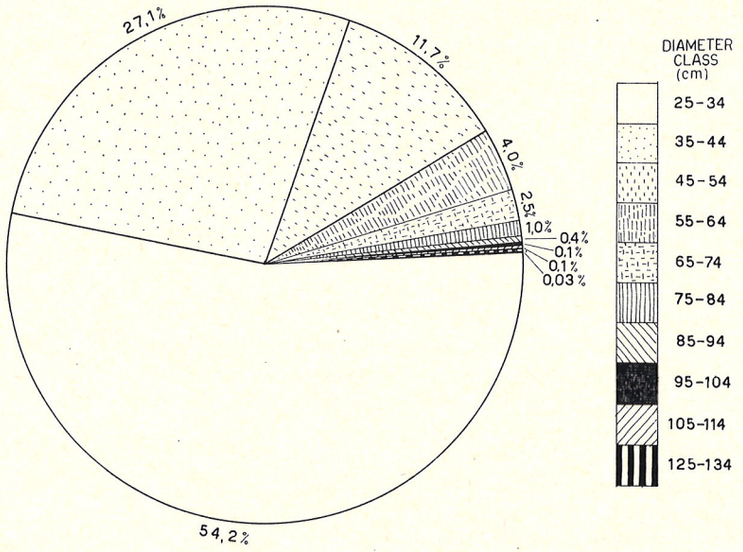

Fig. 2a: Distribution of the trees 25 cm and over in diameter, arranged by diameter class, from the rain forest along the Manaus-Itacoatiara road, Amazonas.

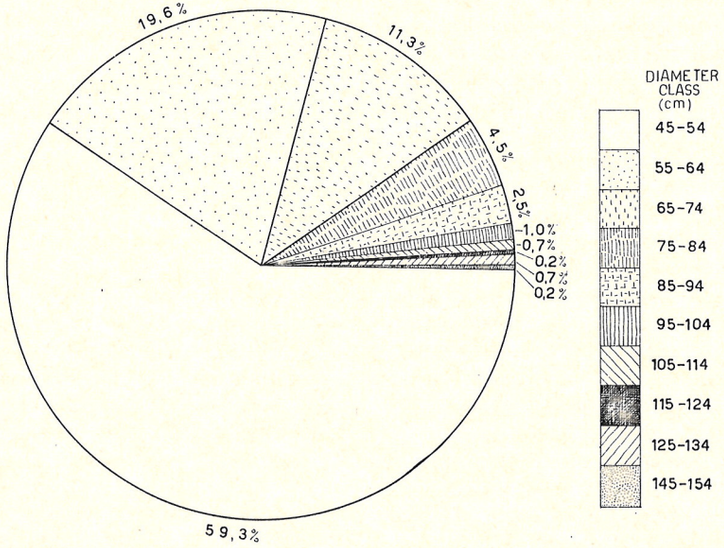

Fig. 2b: Distribution of the trees 45 cm and over in diameter, arranged by diameter class, from the rain forest along the Manaus—Itacoatiara road, Amazonas.

Ocotea spp. (Lauraceae); ucuuba-chico-de-assis — *Osteophloeum platyspermum* (Myristicaceae); abiurana roxa — *Micropholis* sp. (Sapotaceae); Louro gamela — *Nectandra rubra* (Lauraceae); acariquara roxa — *Minquartia guianensis* (Olacaceae); and mandioqueira — *Qualea paraensis* (Vochysiaceae).

No species and no family can be considered dominant or even almost so in the forest around Manaus. However, some of the most important families judging by the number of species and individuals, are obviously the Leguminosae, Chrysobalanaceae, Lauraceae, Sapotaceae and Lecythidaceae. The number of tree families represented in the forest was 47.

In the site of the Walter Egler Forest Reserve, where the present study of the litter-fall was made, some of the most important species of every stratum and life-form are recorded below.

Species of the tree strata:

Angelim pedra, *Dinizia excelsa* (Leguminosae)
Castanha de macaco, *Cariniana micrantha* (Lecythidaceae)
Faveira fôlha fina, *Piptadenia suaveolens* (Leguminosae)
Faveira, *Pithecolobium pedicellare* (Leguminosae)
Angelim rajado, *Pithecolobium racemosum* (Leguminosae)
Cumarurana, *Dipteryx oppositifolia* (Leguminosae)
Tachi vermelho, *Sclerolobium* spp. (Leguminosae)
Guariúba, *Clarisia racemosa* (Moraceae)
Cardeiro, *Scleronema micranthum* (Bombacaceae)
Cupiúba, *Goupia glabra* (Celastraceae)
Faieira, *Roupala montana* (Proteaceae)
Mandioqueira, *Qualea* spp. (Vochysiaceae)
Maueira, *Erisma bicolor* (Vochysiaceae)
Piquiàrana, *Caryocar glabrum* (Caryocaraceae)
Matamatá preto, *Eschweilera odora* (Lecythidaceae)
Acariquara branca, *Geissospermum sericeum* (Apocynaceae)
Breu, *Protium* spp. (Burseraceae)
Macucu chiador, *Licania oblongifolia* (Chrysobalanaceae)
Inharé, *Helicostylis scabra* (Moraceae)
Imbaùbarana, *Pourouma myrmecophylla* (Moraceae)
Louro preto, *Ocotea* spp. (Lauraceae)
Urucurana, *Sloanea* spp. (Elaeocarpaceae)
Cuquirana brava, *Ragala spuria* (Sapotaceae)
Rosada brava, *Micropholis* sp. (Sapotaceae)
Abiurana abiu, *Pouteria guianensis* (Sapotaceae)
Envireira, *Duguetia* sp. (Annonaceae)

Plants of the "shrub" stratum:

Rinorea guianensis (Violaceae)
Neoptychocarpus apodanthus (Flacourtiaceae)
Casearia resinifera (Flacourtiaceae)
Palicourea longiflora and others (Rubiaceae)
Psychotria spp. (Rubiaceae)
Henriettea duckeana (Melastomataceae)
Arumã verdadeiro, *Ischnosiphon* sp. (Marantaceae)

Pseudima frutescens (Sapindaceae)
Espinheiro preto, *Astrocaryum munbaca* (Palmae)
Pupunha brava, *Syagrus inajai* (Palmae)
Marajá da terra firme, *Bactris* sp. (Palmae)

Plants of the ground stratum:

Heliconia acuminata (Musaceae)
Cephaelis sp. (Rubiaceae)
Trichomanes spp. (Hymenophyllaceae)
Selaginella sp. (Selaginellaceae)
Palha vermelha, *Orbignya spectabilis* (Palmae)
Palha branca, *Scheelea* sp. (Palmae)
Bacaba (immature) — *Oenocarpus bacaba* (Palmae)
Bacabinha (immature) — *Oenocarpus minor* (Palmae)
Calathea sp. (Maranthaceae)
Pariana sp. (Gramineae)

Saprophyte:

Leiphaimos obconica (Gentianaceae)

Lianes:

Saracura -muirá, *Ampeloziziphus amazonicus* (Rhamnaceae)
Abuta grandifolia (Menispermaceae)
Abuta rufescens (Menispermaceae)
Unha de gato, *Mimosa spruceana* (Leguminosae)
Strychnos spp. (Loganiaceae)
Arumã canela — *Ischnosiphon* sp. (Maranthaceae)
Salacia sp. (Hippocrateaceae)
Kuhlmaniella laxa (Convolvulaceae)
Dicranostylis spp. (Convolvulaceae)
Viùvinha — *Petraea bracteata* (Verbenaceae)
Bignoniaceae spp.
Cipó titica — *Heteropteris* sp. (Araceae)

Epiphytes:

Guzmania minor var. *minor* (Bromeliaceae)
Maxillaria amazonica (Orchidaceae)
Catasetum gnomus (Orchidaceae)
Rabo de arara, *Norantea guianensis* (Marcgraviaceae)
Polypodium megalophyllum (Polypodiaceae)
Elaphogrossum discolor and others (Polypodiaceae)
Vittaria furcata (Polypodiaceae)
Peperomia spp. (Piperaceae)
Codonanthopsis huebnerii (Gesneriaceae)
Anthurium spp. (Araceae)
Octomeria brevifolia (Orchidaceae)
Philodendron distantilobum, *P. traunii*, *P. goeldi* and others (Araceae)

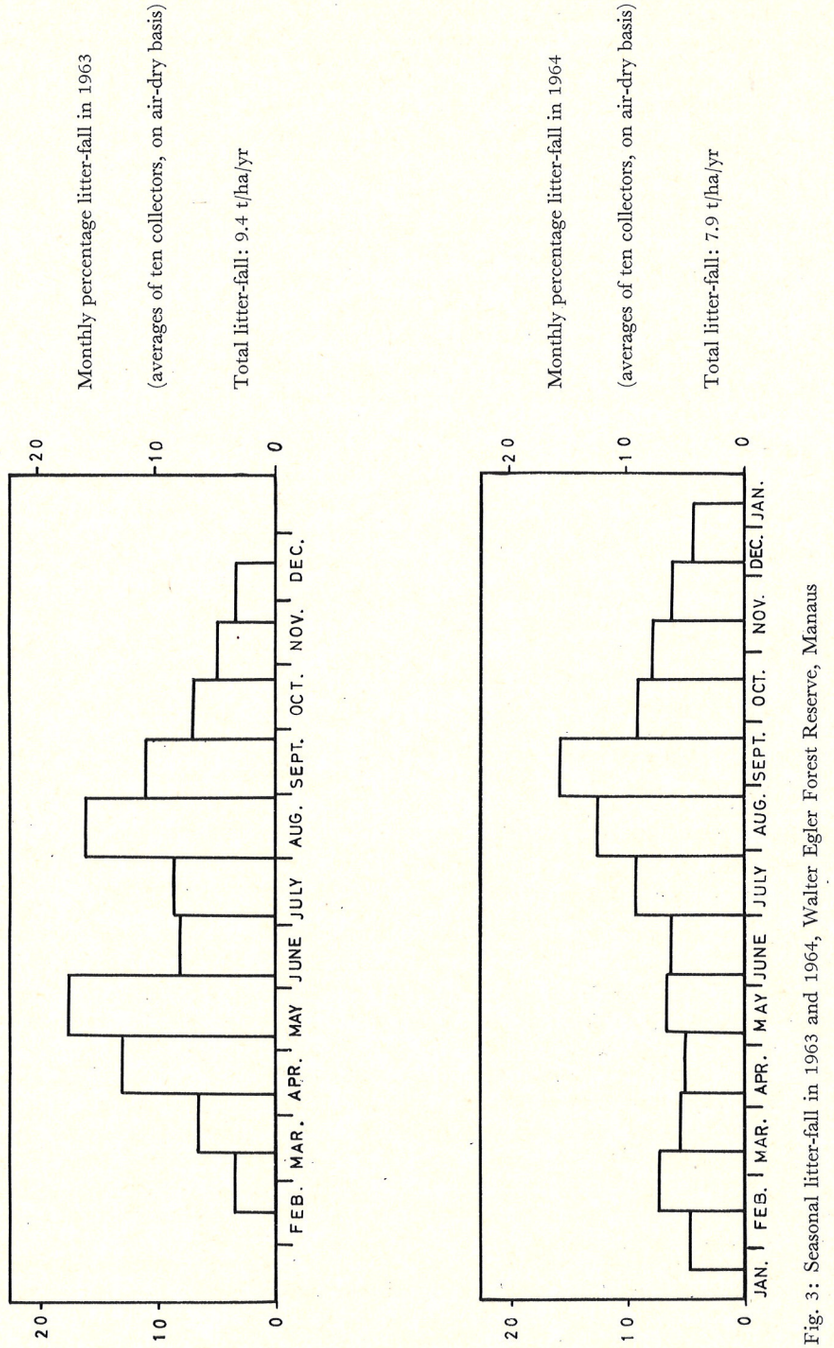

Fig. 3: Seasonal litter-fall in 1963 and 1964, Walter Egler Forest Reserve, Manaus

Results

a) Total litter-fall

No allowance has been made for the fell of bigger branches and stems which contribute a large portion to total dead plant material returned yearly to the forest floor (NYE 1961, NYE and GREENLAND 1960).

As shown in fig. 3, there are marked differences between both years with respect to the height of total litter-fall and its distribution. Furthermore, it is shown that the litter-fall in both years is continuously throughout the year, with maxima in August/September, and in 1963, also in April/May. About fifty per cent of total litter-fall are deposited in the dry, so-called summer period, from June to October.

Total annual litter production in the W. Egler Forest Reserve is inferior to that reported from lowland forests of the Congo and Ghana, but much higher than in forests of Nigeria and the Ivory Coast (table 1). Litter production in the studied Amazonian forest corresponds more or less to that of Dipterocarp and secondary forests of Malaya, of tropical rain forest in Columbia and deciduous forests in Venezuela. The low annual litter production of the Amazonian forest may be correlated with its, by tropical standards, poor quality (MC GRATH et al. 1953, cf. SCHNELL 1961 who citing DUCKE and BLACK 1954 mentioned that Amazonian terra firme forests are lower in height than corresponding African forests, but richer in species (BLACK et al. 1950, MURÇA et al. 1953, RODRIGUES 1967)). ELLENBERG (1959) reported on similar forests of Peruvian Amazonia which in his opinion have a relatively low productivity.

Table 1. Annual Production of Leaf, Other and Total Litter in Tropical Lowland Forests

Location	Type of Forest	Litter-fall (t/ha/yr.) Leaves	Other	Total	Drying Method[1])	Authority
Congo (Yangambi)	*Macrolobium* forest			15.3	A	LAUDELOUT and MEYER (1955)
	Young secondary forest (*Musanga cecropioides*)			14.9	A	LAUDELOUT and MEYER (1955)
	Mixed forest			12.4	A	LAUDELOUT and MEYER (1955)
	Brachystegia laurentii forest			12.3	A	LAUDELOUT and MEYER (1955)
	8-year forest fallow			14.2	A	BARTHOLOMEW et al. (1953)
Ghana (Kade)	Moist semi-deciduous forest	7.0	3.5	10.5	O	NYE (1961)
Nigeria (Ibadan)	Mixed dry forest	3.8	1.8	5.6	A	MADGE (1965)
Ivory Coast (Anguédédou)	Virgin tropical rain forest	2.1	1.9	4.0	O	MÜLLER and NIELSEN (1965)
Colombia (Granja Calima)	Tropical rain forest			8.5	O	JENNY (1948, 1950), JENNY et. al. (1949)
Brazil (Manáus)	Tropical rain forest	6.4	1.5	7.9	O	This study, 1963
		4.8	1.9	6.7	O	This study, 1964
Malaya	Dipterocarp forest			7.2	O	MITCHELL (cited by BRAY and GORHAM 1964)
				5.5	O	
	Secondary forest			10.5	O	MITCHELL (cited by BRAY and GORHAM 1964)
				8.3	O	

[1]) A = Air-dry; O = Oven-dry

Due to the fact that the total annual litter in the Amazonian rain forest averages 7.4 t/ha/yr., the figures of 10 to 12 t/ha/yr. generally accepted for forest in the humid tropics (DOMMERGUES 1963) are too high. MADGE (1965) reported only 5.6 t of litter per ha and year, for a Nigerian forest. MEDINA (1966) reported on 8.25 t dry leaf litter per ha and year measured in a deciduous forest of the central Llanos of Venezuela, varying at different sites between 5.7 and 9.5 t/ha/yr.

In Fig. 4 the rain-fall curve[1]) of 1963 (data from the meteorological station at the nearby A. Ducke Forest Reserve) is compared with the curve of litter-fall in that year of the W. Egler Forest Reserve. This figures shows that litter-fall was highest in May and August, i. e. in the dry season of that exceptionally dry year. The May peak of the litter-fall curve seems to be due to the extraordinarilly early beginning of the dry season which started already in February being interrupted by high rainfall during few days of April due to heavy rain storms (cf. peak of the rain-fall curve in April).

The August peak of the litter-fall curve which is also observed in 1964 (fig. 5) corresponds with the centre of the dry season. At the end of this period, in September and October, the litter-fall diminished and reached its normal level being due to the continuous change of foliage of the evergreen forest trees.

No data on the monthly deposition of litter fractions can be given for 1963, because in that year only ten litter samples each of them collected in one of the ten litter recipients, were shipped to Europe. Weights of annual litter fractions are given at the margin of fig. 4.

For 1964, a clear effect between rain-fall and litter-fall is visible in fig. 5. Litter-fall oscillated around 400 kg/ha/month during the wet season with an average of 227 mm rain-fall/month. At the full start of the dry season (average 72 mm of rain-fall per month), litter-fall increased rapidly culminating in a pronounced maximum in September, by parts due to a high proportion of wood in the litter, and then falling off again. Litter-fall is about two-times higher during the dry season from June to October (average 733 kg per hectare and month), compared with the season from March to June plus November and December (average 383 kg/ha/month).

b) Litter fractions

In 1964 by far the greatest part of total litter consisted of leaves (71.6 per cent) which contributed the largest proportion of total litter during the entire year (fig. 4). Fruits (7.5 per cent of total litter) showed relatively insignificant fluctuations during the year. The culmination of this fraction in March is due to shedding of fruits of some forest tree species in this period. Wood contributed 20.9 per cent of total litter-fall; its seasonal distribution resembles that of leaf-fall.

In 1963 similar data for the three litter fractions in relation to total annual litter have been observed (cf. fig. 4).

The above data on percentage litter fractions are very similar to those reported by NYE (1961) from a mature secondary forest in Ghana (about 67 per cent leaves of 10.5 t/ha/yr. total litter-fall). BRAY and GORHAM (1964) gave also similar data for equatorial forests (about 62 per cent of 10.9 t/ha/yr. consisting in leaves), and MADGE

[1]) Other metereological factors like wind and temperature have not been tested. MAGDE (1965), in a similar study of litter — fall in a forest at Ibadan, Nigeria found no effect between wind and weight of litter—fall (cf. MILLER and HURST 1957).

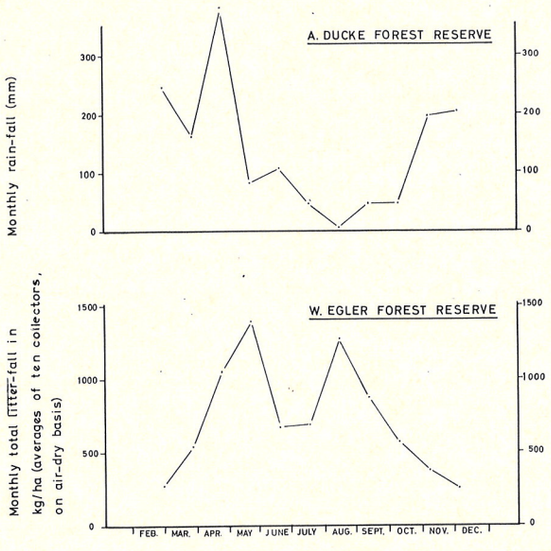

Fig. 4: Seasonal rain-fall and litter-fall in 1963

Total rain-fall: 1,528.9 mm

Annual production (oven-dry matter)

Fraction	t/ha/yr.	% of total
Leaves	6.4	81.0
Fruits	0.2	2.5
Wood	1.3	16.5
Total	7.9	100.0
Termite fraction	0.1	

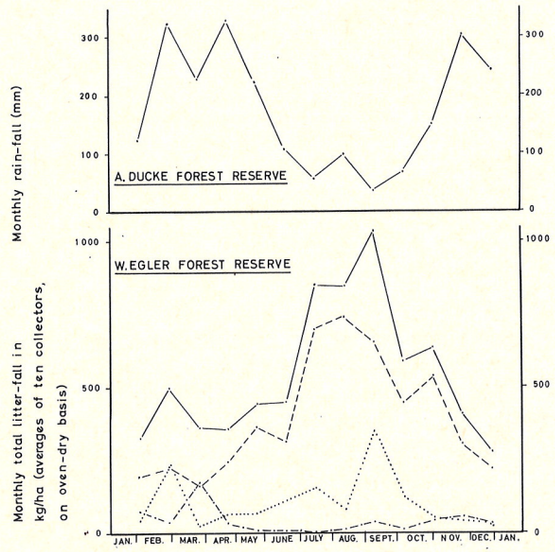

Fig. 5: Seasonal rain-fall and litter-fall in 1964

Annual production (oven-dry matter)

Fraction	t/ha/yr.	% of total
- - - Leaves	4.8	71.6
- - - Fruits	0.5	7.5
..... Wood	1.4	20.9
—— Total	6.7	100.0
Termite fraction	0.009	

(1965) reported on 5.6 t of total litter production per hectare and year in a forest at Ibadan, of which 65 per cent consisted in leaves.

c) Accuracy of measurements

In table 2 standard deviation (S.D.) and percentage standard error (S.E. %) are given for both total litter and litter fractions deposited in 1963 and 1964. Taking a standard error of less than 10 per cent as satisfactory, the number of litter collectors has been too small to give adequate estimates of the fall of wood and fruits as well. Reducing the standard error to ten per cent of the mean would require about hundred measurements of both fractions.

Table 2. Accuracy of Measurements

Litter Fraction	O. M. t/ha/yr.	Range	S. D.	S. E. %
1963				
Leaves	6.4	3.9 — 8.5	1.3	6.6
Wood	1.3	0.3 — 5.5	1.5	36.1
Fruits	0.2	0.04— 1.0	0.3	48.4
Total Litter	7.9	5.1 —11	1.9	7.5
1964				
Leaves	4.8	2.7 —6.4	1.1	7.3
Wood	1.4	0.5 —3.5	0.8	18.1
Fruits	0.5	0.02—2.0	0.4	28.0
Total Litter	6.7	4.0 —9.3	1.6	7.7
Means				
Leaves	5.6		1.5	5.9
Wood	1.3		1.2	20.1
Fruits	0.4		0.4	21.5
Total Litter	7.3		1.9	5.7

Table 3 shows the accuracy of measurements during thirteen litter collection periods in 1964. The differences between the collectors are considerably in all cases; the standard errors oscillate between 8.6 and 42.5 per cent (leaves), 20.7 and 60.8 per cent (wood), 30.7 and 90.4 per cent (fruits), and between 9.5 and 46.5 per cent (total litter).

It is evident that number of collectors, their dimension, and time of observation should be appreciably enlarged to reach accurate mean values.

Table 3. Accuracy of Monthly Litter Measurements in 1964

Month	Number of Collectors	Leaves O. M. t/ha/yr.	Leaves Range	Leaves S. D.	Leaves S. E. %	Wood O. M. kg/ha/month	Wood Range	Wood S. D.	Wood S. E. %
I/II	10	198.0	131.6— 306.0	54.0	8.6	46.8	0— 166.8	64.8	43.8
II/III	10	225.2	143.2— 414.0	77.2	10.8	236.0	0—1,117.6	369.6	46.8
III/IV	10	162.4	58.4— 354.4	78.4	15.2	27.6	0— 114.4	37.6	43
IV/V	10	242.8	140.0— 420.0	131.2	17.1	64.8	0— 225.6	64.4	50.9
V/VI	10	363.2	78.4—1,821.6	488.8	42.5	62.8	0— 268.0	85.6	43.1
VI/VII	10	317.2	120.0— 694.0	154.8	15.6	118.0	0— 430.0	130.4	35.1
VII	10	532.0	243.6—1,308.4	278.0	16.5	124.8	9.2— 343.2	104.4	29.1
VIII	10	739.6	292.4—2,362.4	581.2	24.9	85.6	0— 571.2	164.8	60.8
IX	10	651.2	330.0— 924.4	174.8	8.5	349.2	12.0— 157.8	456.4	41.4
IX/X	10	448.0	130.8—1,049.4	250.8	17.7	125.6	0— 746.8	212.8	53.6
X/XI	10	396.8	43.2— 952.4	256.8	20.7	39.6	0— 127.2	33.6	20.7
XI/XII	10	309.2	120.4— 840.4	238.0	19.2	41.6	0— 196.4	55.2	42.3
XII/I	10	221.2	122.8— 372.4	80.0	11.5	34.0	0— 156.4	46.4	43.2

Month	Number of Collectors	Fruits O. M. kg/ha/yr.	Fruits Range	Fruits S. D.	Fruits S. E. %	Total Litter O. M. kg/ha/yr.	Total Litter Range	Total Litter S. D.	Total Litter S. E. %
I/II	10	78.4	0— 393.2	120.4	48.6	321.1	141.6— 592.8	162	16
II/III	10	38.8	0— 203.2	61.1	49.8	500	182.4—1,331.2	370.9	23.5
III/IV	10	171.2	0—1,514.0	488.8	90.4	361.2	78.0—1,943.6	530.8	46.5
IV/V	10	36.4	0— 200.4	65.9	57.3	344.0	156.8— 544.0	133.8	12.3
V/VI	10	13.6	0— 79.6	24.8	57.6	439.6	129.6—1,929.2	507.5	36.5
VI/VII	10	12.0	0— 78.0	23.6	62.2	442.8	210.4— 855.2	185.5	13.3
VII	10	2.4	0— 16.0	5.0	65.8	637.2	254.4—1,552.4	362.0	18.0
VIII	10	16.8	0— 110.8	33.9	63.8	842.0	305.6—2,399.6	619.1	23.3
IX	10	38.4	0— 83.6	36.5	30.7	1,038.8	370.8—2,502.4	311.6	9.5
IX/X	10	14.4	0— 28.8	11.1	30.8	588.0	289.6—1,119.2	255.5	13.8
X/XI	10	32.0	0— 236.4	68.7	67.9	464.0	52.8—1,095.2	301.4	20.6
XI/XII	10	59.6	0— 370.4	107.2	56.9	410.4	128.0—1,105.2	309.5	23.9
XII/I	10	24.0	0— 156.4	45.8	60.4	279.2	130.8— 410.0	97.5	11.0

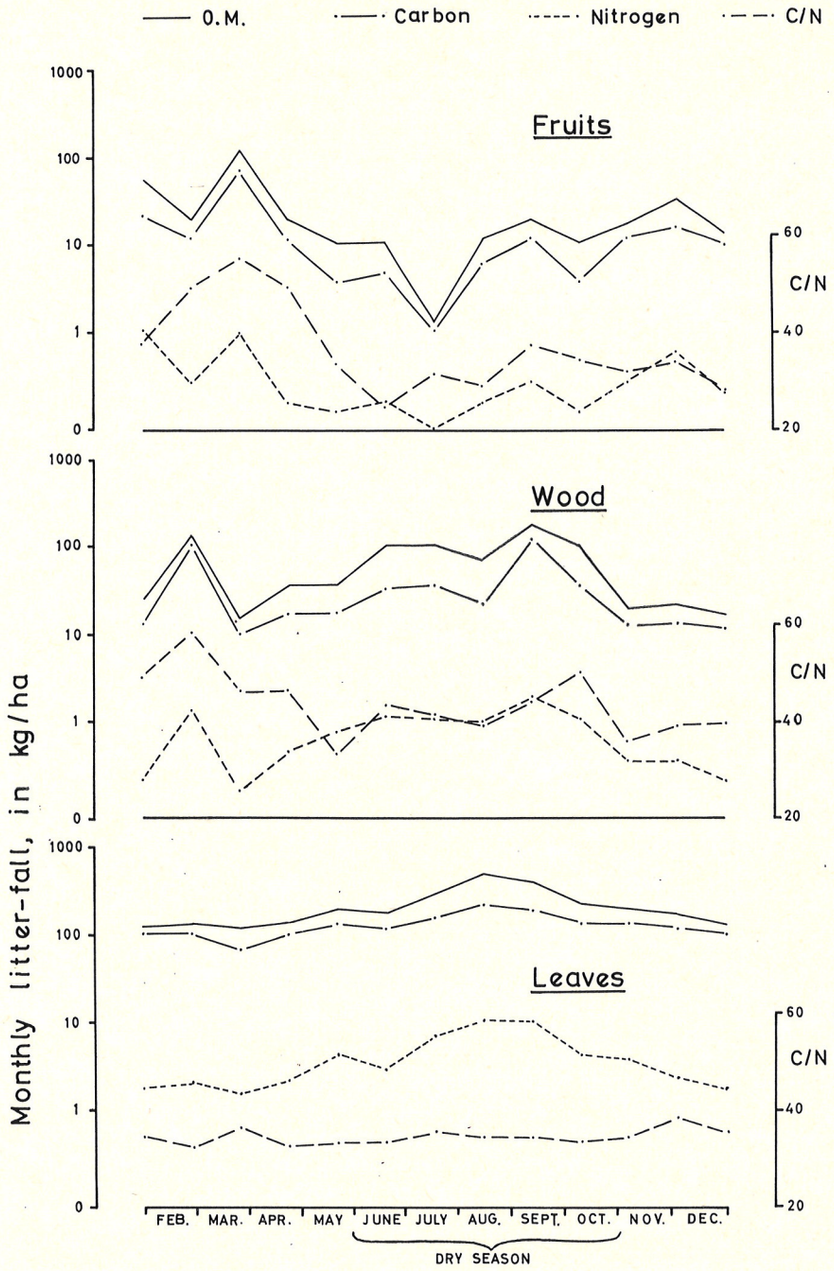

Fig. 6: Seasonal fall of litter fractions in 1964

d) Organic carbon and total nitrogen content of the litter

In fig. 6, the seasonal variations of organic carbon, total nitrogen and C/N ratios of the three litter fractions collected in 1964 are also shown.

The carbon and nitrogen curves of leaves run more or less parallel each to each other and to the total organic matter curve as well resulting a C/N ratio of about 35 : 1 being nearly constant throughout the year.

There is no such a good correspondence between organic matter, organic carbon and total nitrogen in the case of the wood fraction. The C/N ratio being wider than that of leaves oscillates between 35 and 60 : 1.

The proportion of fruits to total litter is considerably variable throughout the year which will be due to shedding of fruits by different tree species in different periods. In contrast to leaves, there seems to be no relation between amount of both fruits and wood and annual seasons. Differences between the amount of nitrogen returned to the soil in the various months are considerable, resulting a wide range of the C/N ratio.

There are no significant differences between the nitrogen contents (expressed as per cent of organic matter) of the monthly litter-fall.

Table 4. Organic Carbon and Total Nitrogen Contents of Annual Litter Fractions and Total Litter as well

Litter Fraction	O. M.	1963 C		N		C/N[1]
	t/ha/yr.	kg/ha/yr.	% O.M.	kg/ha/yr.	% O.M.	
Leaves	6.4	3,334	52.1	96.5	1.5	34.5
Wood	1.3	601	46.2	15.6	1.2	37.8
Fruits	0.2	88	44.0	1.84	0.9	35.4
Total Litter	7.9	4,023	50.9	113.9	1.4	35.9
Termite Fraction	0.1	34	34	1.1	1.1	31.9

Litter Fraction	O. M.	1964 C		N		C/N[1]
	t/ha/yr.	kg/ha/yr.	% O.M.	kg/ha/yr.	% O.M.	
Leaves	4.8	2,612	54.4	76.0	1.6	34.5
Wood	1.4	680	48.6	14.8	1.1	43.8
Fruits	0.5	268	53.6	6.4	1.3	37
Total Litter	6.7	3,560	53,1	97.2	1.5	38.4
Termite Fraction	0.009	4	44.4	0.1	1.1	30.8

Litter Fraction	O. M.	Mean C		N		C/N
	t/ha/yr.	kg/ha/yr.	% O.M.	kg/ha/yr.	% O.M.	
Leaves	5.6	2,973	53.1	86.3	1.5	34.5
Wood	1.4	641	45.8	15.2	1.1	40.8
Fruits	0.4	178	44.5	4.1	1.0	36.2
Total Litter	7.4	3,792	51.2	105.6	1.4	37.2
Termite Fraction	0.1	38	38.0	1.2	1.2	31.4

[1]) Calculated from both determined mg C and mg N in original samples.

Table 5. Organic Carbon and Total Nitrogen Content of Litter of Tropical Forests Together with Data from Other Parts of the World for Comparison

Region (Authority)	Forest	Litter	Organic Carbon[1]) kg/ha/yr.	Organic Carbon[1]) per cent O. M.	Total Nitrogen kg/ha/yr.	Total Nitrogen per cent O. M.	C/N
Congo, Yangambi (Laudelout and Meyer 1955)							
	Mixed Forest	Total	6,200	50	224	1.8	28
	Brachystegia Forest	Litter, dry	6,150	50	223	1.8	28
	Macrolobium Forest		7,650	50	154	1.0	50
	Secondary Forest		7,450	50	140	0.9	53
Ghana, Kade (Nye 1961, Nye and Greenland 1960)							
	High Forest	Total litter, oven-dry	5,250	50	199	1.9	26
Senegal, Casamance (Maheut and Dommergues 1960)							
	Teak Plantation	Leaf litter, dry	2,900	50	38	0.7	76
			2,350	50	44	0.9	53
Colombia, Calima (Jenny 1950)							
	Broad-leaved Rain forest	Total litter, oven-dry	3,910	45.9	104	1.2	38
Chinchiná	Broad-leaved Forest		5,100	50.4	157	1.6	33
Thailand[2]) (Ogawa et al. 1961)							
	Dipterocarp Savanna F.	Total litter	4,500	57.7	120	2.7	37
	Mixed Savanna F.		4,500	56.3	130	2.9	35
	Evergreen Gallery F.		14,600	57.7	360	2.5	41
	Temperate Evergreen F.		10,400	55.0	200	1.9	52
South Carolina (Metz 1952)							
	Pine	Leaf litter, oven-dry	2,100	50	11.3	0.3	185
	Pine-Hardwood		1,950	50	26.4	0.7	74
	Hardwood		2,150	50	29.7	0.7	72
California (Jenny 1950)							
	Shave-oak Forest	Total litter	746	48.1	12.7	0.8	59
	Shave-pine Forest		1,640	52.1	15.4	0.5	106
U. S. A. (Lutz and Chandler 1946)							
	Deciduous F.	Total litter	1—1,500	50	19	1.3—1.9	53—79
	Conifer F.				26	1.7—2.6	39—58
New Zealand, North Island (Miller and Hurst 1956)							
	Nothofagus truncata F.	Leaf litter, oven-dry	1,184	56.4	12.6	0.6	94
		Twig litter, oven-dry	745	53.2	5.6	0.4	133
(Will 1959)	*Pinus radiata* Pl.	Total litter, dry	2,800	50	37.7	0.7	74
	Pinus nigra Plantation		3,950	50	36.2	0.5	109
	Pseudotsuga taxifolia Pl.		1,450	50	22	0.8	66
	Larix decidua Plantation		1,850	50	26.9	0.7	69
Southern Queensland (Webb 1958)							
	Nothophyll Vine F.	Leaf litter, oven-dry	3,350	50	108	1.6	31
	Simple Nothophyll Vine F.		1,750	50	36	1.1	47

[1]) If no data on organic carbon were given by the authors, the carbon content of the litter is calculated at a rate of fifty percent C in litter.

[2]) Data given by the authors are estimates only.

Table 4 gives the organic carbon and total nitrogen contents of litter fractions and total litter for both sampled years, and the corresponding averages as well. In both years, leaves were richer in both carbon and nitrogen as well and had a relatively narrow C/N ratio. The C/N ratio of fruits was similar to that of leaves, that of wood being the widest of all. Both years show differences between absolute and percentage contents of carbon and nitrogen as well.

In table 5, data on organic carbon and total nitrogen and the C/N ratio as well of litter from tropical forsts are given. Comparing the data in table 5 with those of table 4 one can see that forest litter contains about fifty per cent carbon in all cases, but different amounts of nitrogen. Generally, there is a relatively high nitrogen content of 1.5 to 2 per cent in the organic matter of tropical forest litter (Laudelout and Meyer 1955, Lemée 1961, Jenny 1950, Nye 1961), resulting a rather narrow C/N ratio. The elevated nitrogen content of tropical forest litter may be related to high fixation of atmospheric nitrogen by symbiotic and non-symbiotic micro-organisms including bluegreen algae.

By means of these nitrogen fixing species the nitrogen house-hold of tropical forests may be quickly re-organized after felling and/or burning of the trees (Ellenberg 1959, 1964), so that the forest regenerates. The secondary forest, however, is different from the original one, in respect to its sociology and productivity which is demonstrated in large areas of Amazonia covered by poor so-called "capoeira". But there are too well growing high secondary forests standing on terra preta soils which are very rich in phosphorus. So it may be concluded that the regeneration of Amazonian forests depends mainly upon the phosphorus content of the soil.

The litter of Amazonian forests is lower in nitrogen than other tropical forest litter (Dommergues 1963, D'Hoore 1961). The exceptionally high nitrogen content of forest litter of Thailand (Ogawa et al. 1961) has been estimated only.

Resumo

Em 1963 e 1964 mediu-se a produção de manta vegetal numa mata de terra firme da Reserva Walter Egler, localizada a nordeste de Manaus, na estrada Manaus-Itacoatiara, Km 65.

Em meio hectare de mata foram distribuídas dez caixas de madeira para coleta da manta produzida por detritos vegetais que caiam.

As amostras obtidas foram posteriormente despachadas para a Europe e analisadas no Laboratório de Solos do Departamento de Ecologia Tropical (Instituto de Limnologia do Max Planck).

As amostras foram inteiramente fracionadas a mão em:

i) Fôlhas
ii) Detritos de madeira (ramos, raminhos e casca)
iii) Frutos, flôres, escamas de gema, sementes etc, inclusive restos vegetais irreconhecíveis

As amostras foram em seguida moídas, secadas a 105° C e pesadas.

Determinou-se o carbono orgânico total por combustão úmida com ácido crômico, avaliando-o colorimètricamente. Usou-se a técnica de Kjeldahl para se calcular o nitrogênio total.

A mata é típicamente amazônica, de solo argiloso, florísticamente muito heterogênea. A altura média do dossel da mata é em tôrno de 25 m.

Produziu a mata 7,4 toneladas métricas de manta vegetal total por hectare e ano. A folhagem contribuiu com 75,7% e outros detritos orgânicos, 24,3%.

A queda de detritos ocorreu durante todo o ano. Durante a estação sêca de junho a outubro, a manta formada correspondeu a cêrca de 50% da produção anual. A maior produção mensal de manta (1.04 t/ha) verificou-se em setembro de 1964, sendo o mês mais sêco daquele ano. Cêrca de meia tonelada de manta por mês ocorreu durante a estação das chuvas. 3,8 toneladas de carbono orgânico e 106 Kg de nitrogênio voltaram ao solo anualmente, correspondendo a 51,2 e 1,4% respectivamente da manta total.

Os dados aqui assinalados são médias de dois anos.

References

BARTHOLOMEW, W. V., MEYER, J., and LAUDELOUT, H. (1953): Mineral nutrient immobilization under forest and grass fallow in the Yangambi (Belgian Congo) region. 27 p. (Publs Inst. natn. Etude agron. Congo belge, Série Scient. no. 57).

BLACK, G. A., DOBZHANSKY, TH., and PAVON, D. (1950): Some attempts to estimate species diversity and population density of trees in Amazonian forests. Bot. Gaz., vol. 111, no. 4, p. 413—425.

BRAY, J. R., and GORHAM, E. (1964): Litter production in forests of the world. In: J. B. CRAGG (ed.) Adv. ecol. Res., vol. 2, p. 101—157.

DUCKE, A., and BLACK, G. A. (1954): Notas sôbre a fitogeografia da Amazônia brasileira. 62 p. (Bolm tec. Inst. agron. N, no. 29).

DOMMERGUES, Y. (1963): Les cycles biogéochimiques des éléments minéraux dans les formations tropicales. Bois Fôrets Trop., no. 87, p. 9—25.

D'HOORE, J. (1961): Influence de la mise en culture sur l'évolution des sols dans la zone de fôret dense de basse et moyenne altitude. In: Unesco (ed.) Proc. Abidjan Symposium 1959, Humid Tropics Research, p. 49—58.

ELLENBERG, H. (1959): Typen tropischer Urwälder in Peru. Schweiz. Z. Forstwes., no. 3, p. 169—187.

ELLENBERG, H. (1964): Stickstoff als Standortsfaktor. Ber. dt. bot. Ges., vol. 77, no. 3, p. 82—92.

JENNY, H. (1948): Great soil groups in the equatorial regions of Colombia, South America. Soil Sci. vol. 66, p. 5—28.

JENNY, H. (1950): Causes of high nitrogen and organic matter content of certain tropical forest soils. Soil Sci., vol. 69, p. 63—69.

JENNY, H., GESSEL, S. P., and BINGHAM, F. T. (1949): Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci., vol. 68, p. 419—432.

LAUDELOUT, H. (1961): Dynamics of tropical soils in relation to their fallowing techniques. 111 p. Rome, FAO.

LAUDELOUT, H., and MEYER, J. (1955): Les cycles d'éléments minéraux et de matière organique en forêt équatoriale congolaise. In: Trans. 5th int. Congr. Soil Sci., Léopoldville 1954, vol. 2, p. 267—272.

LEMEE, G. (1961): Effets des caractères du sol sur la localisation de la végétation en zone équatorial et tropicale humide. In: Unesco (ed.) Proc. Abidjan Symposium 1959, Humid Tropics Research, p. 25—39.

LUTZ, H. I., and CHANDLER, R. F. (1946): Forest Soils. New York, Wiley. 514 p.

MAGDE, D. S. (1965): Leaf fall and litter disappearance in a tropical forest. Pedobiologia, vol. 5, no. 4, p. 273—288.

MAHEUT, I., and DOMMERGUES, Y. (1960): Les teckeraies de Casamance. Bois Fôrets Trop., vol. 70, p. 25—42.

MCGRATH, K., GACHOT, R., and GALLANT, N. M. (1953): The Amanzon valley. Unasylva, vol. 7, no. 3, p. 99—104.

MEDINA, E. (1966): Producción de hojarasca, respiración edáfica y productividad vegetal en bosques deciduos de los Llanos centrales de Venezuela. In: E. A. RAPOPORT (ed.) Progresos en biología del suelo, Monografía I Centro Coop. cient. UNESCO Amer. Lat., Montevideo 1966, p. 97—108.

METZ, L. J. (1952): Weight and nitrogen and calcium content of the annual litter fall of forests in the South Carolina piedmont. Proc. Soil Sci. Soc. Am., vol. 16, p. 38—41.

MILLER, R. B., and HURST, F. B. (1957): The quantity nutrient content of hard beach litter. 14 p. (N. Z. For. Res. Notes no. 8, Soil Bur. Publ. no. 114).

MÜLLER, D., and NIELSEN, J. (1955): Production brute, pertes par respiration et production nette dans la forêt ombrophile tropicale. Forst. ForsVaes. Danm., vol. 29, p. 69—160.

MURSA PIRES, J., DOBZHANSKY, TH., and BLACK, G. A. (1953): An estimate of the number of species of trees in an Amazonian forest community. Bot. Gaz., vol. 114, no. 4, p. 467—477.

NYE, P. H. (1961): Organic matter and nutrient cycles under moist tropical forest. Pl. Soil, vol. 12, no. 4, p. 333—346.

NYE, P. H., and GREENLAND, D. J. (1960): The soil under shifting cultivation. 156 p. (Tech. Commun. Commonw. Bur. Soil Sci. no. 51).

OGAWA, H., YODA, K., and KIRA, T. (1961): A preliminary survey on the vegetation of Thailand. In: Kira, T. and T. Umesao (ed.) Nature and life in Southeast Asia. vol. 1, p. 21—157.

RIEHM, H., and ULRICH, B. (1950): Quantitative kolorimetrische Bestimmung der organischen Substanz im Boden. Landw. Forsch., vol. 6, no. 3, p. 173—176.

RODRIGUES, W. A. (1967): Inventário florestal pilôto ao longo da Estrada Manaus-Itacoatiara, Estado do Amazonas. Dados preliminares. Ata do simpósio sôbre a Biota Amazônica, Belém 1966, vol. 7 (Conservação da Natureza e Recursos Naturais), p. 257—267.

SCHNELL, R. (1961): Le problème des homologies phytogéographiques entre l'Afrique et l'Amérique tropicales. Mém. Mus. natn. Hist. nat., Paris, Sér. B. Bot., vol. 11, no. 2, p. 137—242.

WEBB, L. J. (1958): Note on the studies on rain-forest vegetation in Australia. In: Unesco (ed.) Proc. Kandy Symposium 1956, Humid Tropics Research, p. 171—174.

WILL, G. M. (1959): Nutrient return in litter and rainfall under some exotic conifer stands in New Zealand. N. Z. Jl agric. Res., vol. 2, p. 719—734.